

SEASONAL RANGES AND SITE FIDELITY OF ADULT MALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN SOUTHERN TEXAS

MICKEY W. HELLICKSON, TYLER A. CAMPBELL,* KARL V. MILLER, R. LARRY MARCHINTON, AND CHARLES A. DEYOUNG

Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602 (MWH, KVM, RLM)
United States Department of Agriculture, Animal Plant Health Inspection Service, Wildlife Services, National Wildlife
Research Center, Texas A&M University-Kingsville, Kingsville, TX 78363 (TAC)

Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363 (CAD)

Present address of MWH: King Ranch Production Office, P.O. Box 1090, Kingsville, TX 78364

*Correspondent: tyler.a.campbell@aphis.usda.gov

ABSTRACT—Much is known about movements of female white-tailed deer (*Odocoileus virginianus*). However, relatively few investigations have been directed toward free-ranging male deer and even fewer have involved mature (≥ 4 years old) males. Our objectives were to characterize utilization distributions and site fidelity, and to evaluate the subdominant-dominant-floater model using an extensive radiotelemetry dataset collected from male deer ≥ 1.5 years old in southern Texas. We generated home ranges and core areas of 96 males from 16,696 location estimates collected during January 1993–June 1995. Annual home-range size did not differ among age categories. Males maintained smaller home ranges during spring than during other seasons and old males (≥ 7 years old) displayed smaller seasonal home ranges than young or mature males. Deer exhibited greater fidelity to home range during summer than during spring, pre-rut, and rut seasons. We detected limited evidence supporting the subdominant-dominant-floater model. The high fidelity to home range between years that we saw suggests little between-year shifting; however, annual home-range sizes exceeded the acreage of most private landholdings, which should be considered when formulating management plans.

RESUMEN—Existe un amplio conocimiento sobre los patrones de movimiento de las hembras de venado de cola blanca (*Odocoileus virginianus*). Sin embargo, pocas investigaciones se han enfocado en estudiar a venados machos silvestres y menos aún a machos maduros (≥ 4 años). Nuestros objetivos fueron caracterizar las distribuciones de uso y fidelidad al sitio, y evaluar el modelo subdominante-dominante-flotante utilizando una extensa base de datos de telemetría de venados machos ≥ 1.5 años de edad en el sur de Texas. Generamos ámbitos hogareños y áreas núcleo para 96 machos de 16,696 ubicaciones estimadas colectadas entre enero de 1993 y junio de 1995. El tamaño del ámbito hogareño anual entre las categorías de edad no fue diferente. Los machos mantuvieron ámbitos hogareños más pequeños durante la primavera que en las otras estaciones y los machos viejos (≥ 7 años) mostraron ámbitos hogareños estacionales más pequeños que los de machos jóvenes o maduros. Los venados mostraron mayor fidelidad al ámbito hogareño durante el verano que durante la primavera, antes de la estación reproductiva y durante la estación reproductiva. Encontramos evidencia limitada que apoya el modelo subdominante-dominante-flotante. La alta fidelidad observada al ámbito hogareño entre años sugiere poco cambio de un año a otro; sin embargo, los tamaños anuales de los ámbitos hogareños excedieron el tamaño de la mayoría de las tierras privadas, lo cual debe ser considerado cuando se diseñen planes de manejo.

Much is known about movements of female white-tailed deer (*Odocoileus virginianus*; Hölzenbein and Schwede, 1989; VerCauteren and Hygnstrom, 1998; Campbell et al., 2004b). However, relatively few investigations have been directed toward free-ranging males and even fewer have involved mature (≥ 4 years old) males. In many

areas, mature males are scarce and researchers have had difficulty in capturing sufficient numbers for study (e.g., Campbell et al., 2005). Numerous properties in southern Texas are exceptions because for decades landowners have implemented management strategies to promote physically mature male deer (Brothers and Ray, 1975).

Brown (1971) observed four behavior patterns that corresponded to the degree of maturation of mature male deer during a radiotelemetry study in southern Texas. First, immature deer formed part of the social group of their mothers. Consequently, their home ranges were similar to those of their mothers and relatively small. Second, young adults separated from the social group of their mothers and became subdominant floaters, associating with various groups and maintaining large home ranges with low site fidelity. Third, middle-aged deer (i.e., fraternal bucks or core animals) formed stable all-male groups and displayed small home ranges with high site fidelity. Fourth, large mature deer did not form permanent associations, becoming dominant floaters; they made frequent trips and maintained large home ranges with low site fidelity. Subsequent investigations have not yielded definitive size of home range and dominance relationships for white-tailed deer. For example, Inglis et al. (1986) identified one subdominant floater and one dominant floater on the Welder Wildlife Refuge ($n = 15$) and no floaters on the San Pedro Ranch ($n = 12$). Furthermore, Brown (1971) was limited by sample size ($n = 9$ radiocollared deer described). Consequently, it is not clear how applicable the observations and management recommendations of Brown (1971) are to other populations with a well-developed age structure for males in southern Texas and elsewhere.

Our objectives were to characterize utilization distributions and site fidelity, and to evaluate the subdominant-dominant-floater model of Brown (1971), which was further developed by Inglis et al. (1986), using an extensive radiotelemetry dataset collected from different-aged adult males in southern Texas. Following the subdominant-dominant-floater model, we expected annual and seasonal sizes of home ranges to be greater in young and mature deer than middle-aged deer. Furthermore, we expected annual and seasonal fidelity to home range to be less in young and mature deer than in middle-aged deer.

MATERIALS AND METHODS—Our research occurred on the 18,020-ha Faith Ranch (28°13'N, 99°56'W) in Dimmit and Webb counties of southern Texas. Mean annual minimum and maximum temperatures were 15 and 29°C, respectively, with summer temperatures often >38°C and winter temperatures rarely below freezing. Mean annual precipitation was 54.6 cm with

most occurring in May and September (National Oceanic and Atmospheric Administration, 1993–1995).

Terrain was gently rolling, dominated by honey mesquite (*Prosopis glandulosa*), guajillo (*Acacia berlandieri*), blackbrush acacia (*Acacia rigidula*), prickly pear cactus (*Opuntia lindheimeri*), and tasajillo cactus (*Opuntia leptocaulis*). Twisted acacia (*Acacia schaffneri*), guayacan (*Porteria angustifolia*), lotebush (*Zizyphus obtusifolia*), kidneywood (*Eysenhardtia texana*), spiny hackberry (*Celtis pallida*), and whitebrush (*Aloysia gratissima*) also were abundant. Dominant grasses included red grama (*Bouteloua trifida*), pink pappusgrass (*Pappophorum bicolor*), threeawn grass (*Aristida*), and buffalograss (*Cenchrus ciliaris*). Common forbs included western ragweed (*Ambrosia psilostachya*), goldenweed (*Isocoma*), bundleflowers (*Desmanthus*), crotons (*Croton*), bladder-pods (*Lesquerella*), and plantain (*Plantago*).

During 1992–1994, we captured adult (≥ 1.5 years old) male white-tailed deer during October using helicopter drive-net (Beasom et al., 1980) or net-gun (DeYoung, 1988) techniques. We randomly selected deer for capture to reduce bias (Leon et al., 1987). We used physical restraint to immobilize deer during handling. One observer estimated age of all captured deer by tooth eruption, replacement, and wear (Severinghaus, 1949), then we grouped deer into four age categories (DeYoung, 1989) based on estimated age at capture: young, 1–2 years old; middle, 3–4 years old; mature, 5–6 years old; old, ≥ 7 years old. For all analyses, we assumed a 1 July birthday of each cohort (Illige, 1951). Additionally, we ear-tagged and radio-collared (Advanced Telemetry Systems, Isanti, Minnesota) all deer when captured.

We collected nocturnal, crepuscular, and diurnal radiotelemetry data during all months of the year. We staggered the beginning of our radiotelemetry route daily to ensure uniform sampling of each deer over a 24-h period. We estimated locations, using radio-receivers and hand-held, 4-element Yagi antennas, by recording 3–5 compass azimuths ≤ 15 min apart from fixed geo-referenced telemetry stations. We used program LOAS (Ecological Software Solutions, Sacramento, California) to generate UTM coordinates and error ellipse areas of estimated locations. We considered individual locations ≥ 4 h apart independent (Swihart and Slade, 1985) and attempted to locate each individual 3–4 times/week. To increase accuracy, we omitted all estimated locations in which the error ellipse area was ≥ 5 ha.

We used the Animal Movement extension (Hooge and Eichenlaub, 1997) of ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California) to generate utilization distributions. We used the fixed-kernel method (Worton, 1989) to generate 95% home range and 50% core areas. We generated estimates of home range and core areas for summer (1 June–30 September), prerut (1 October–31 November), rut (1 December–10 January), postrut (11 January–31 March), spring (1 April–31 May), and annually (July–June). For both annual and seasonal distributions we used least-square cross validation as the smoothing parameter (Silverman, 1986). We only included deer in analyses if they were radiomonitored throughout a year or season.

TABLE 1—Annual size of range (ha; 95 and 50% kernel) of male white-tailed deer (*Odocoileus virginianus*), July 1993–June 1994 and July 1994–June 1995, on the Faith Ranch in southern Texas.

Age	n	95% kernel (ha)	50% kernel (ha)
		Mean (SE)	Mean (SE)
Young (2 years old)	6	922 (328)	144 (47)
Middle (3–4 years old)	12	499 (130)	73 (18)
Mature (5–6 years old)	23	553 (118)	85 (19)
Old (≥ 7 years old)	13	427 (40)	61 (7)

We quantified between-year site fidelity following Campbell et al. (2004a) by calculating the home range and core areas that were reused (i.e., overlap) in the following year or season of the following year using the fixed-kernel method. We used the Spatial Analyst extension of ARCVIEW to determine overlapping areas. We determined percentage overlap by dividing the area of overlap by the mean of the associated home range or core areas and multiplying by 100%. We square-root-transformed percentage data prior to analysis (Steel and Torrie, 1980).

We used a randomized complete-block analysis of variance (ANOVA) to compare fixed-kernel estimates of sizes of annual 95% home range and 50% core area among age categories (SAS Institute, Inc., 2000). Our model considered age as the main effect and deer as the blocking factor. We blocked by deer to make the analysis more sensitive by removing variation among deer from the error term (Kuehl, 1994). To determine differences in percentage overlap in home range and core areas between years, we used a completely randomized ANOVA.

We used a 2-factor ANOVA with blocking to determine differences in seasonal home range and core area sizes among age categories. To compare percentage overlap in home range and core area by season among age categories, we used a 2-factor ANOVA with blocking. In both models we considered age and season as main effects and deer as the blocking factor. For all ANOVA models we accepted statistical significance at $\alpha = 0.1$ to reduce the probability of a Type II error given the small sample size within treatments (Dowdy and Weardon, 1991), and we used Tukey's honestly significant difference as a multiple-range test.

RESULTS—We generated home ranges and core areas of 96 male white-tailed deer ≥ 1.5 years old from 16,696 location estimates collected January 1993–June 1995. Annual size of home range and core areas did not differ among age categories (both $F_{3,11} \leq 1.81$, both $P \geq 0.203$; Table 1). However, between-year overlap in home range varied among age category ($F_{2,11} = 3.50$, $P = 0.067$), with old males displaying greater fidelity to home range than middle-aged males (Table 2). Differences did not occur in fixed-kernel estimates of overlap in core area between-years among age categories ($F_{2,11} = 1.71$, $P = 0.226$).

The interaction of season-by-age category did not vary for size of home range area ($F_{12,394} = 0.50$, $P = 0.914$) or core area ($F_{12,394} = 1.01$, $P = 0.436$). Deer maintained smaller home range areas ($F_{4,394} = 4.03$, $P = 0.003$) during spring than during other seasons and old males displayed smaller home range areas ($F_{3,394} = 2.42$, $P = 0.065$) than both young and mature males (Table 3). Deer exhibited smaller core areas ($F_{4,394} = 8.05$, $P < 0.001$) during spring than during prerut, rut, and postrut seasons. Different-aged males did not vary in size of core area among seasons ($F_{3,394} = 1.71$, $P = 0.163$).

For our analysis of between-year seasonal home range and core area overlap, the interactions of season-by-age category were not significant (both $F_{9,78} \leq 0.79$, both $P \geq 0.623$). Overlap in home range varied seasonally ($F_{4,78} = 3.81$, $P = 0.007$). Deer displayed greater fidelity to home range during summer than during spring, prerut, and rut seasons (Table 4). Different-aged males did not vary in overlap of home range among seasons ($F_{3,78} = 0.30$, $P = 0.824$). Seasonal differences occurred in overlap of core area ($F_{4,78} = 2.82$, $P = 0.030$). Deer exhibited less fidelity to core area during rut than during spring, summer, and postrut seasons. Seasonal overlap in core area did not vary by age category ($F_{3,78} = 1.35$, $P = 0.265$).

DISCUSSION—Annual home-range sizes of male white-tailed deer in southern latitudes of the United States are reported to be 700–1,511 ha (Miller et al., 2003). Our estimates of home-range size compared favorably, generally occurring on the lower end of the reported range. Although statistical comparisons are most appropriately conducted on core areas of activity (Hooze and Eichenlaub, 1997), few investigations have reported sizes of core area for free-ranging males. In the Florida Keys, Lopez et al. (2003) reported that core areas of males were ≤ 29 ha during periods

TABLE 2—Mean (*SE*) between-year overlap in home range (95% kernel) and core area (50% kernel; %—a measure of site fidelity) of male white-tailed deer (*Odocoileus virginianus*), July 1993–June 1994 and July 1994–June 1995, on the Faith Ranch in southern Texas.

Age (during second year of radiomonitoring)	<i>n</i>	95% kernel (%) Mean (<i>SE</i>)	50% kernel (%) Mean (<i>SE</i>)
Middle (3–4 years old)	4	61 (5)	67 (5)
Mature (5–6 years old)	4	66 (4)	59 (6)
Old (≥7 years old)	6	73 (2)	45 (11)

of range expansion associated with hurricane activity. Our estimates of core-area sizes were 2 times greater than this and likely reflect general differences between insular and mainland populations. However, Webb (2005) found comparatively small annual core areas of ≤34 ha for mature males near our study site. These findings further illustrate the behavioral plasticity of white-tailed deer (Miller, 1997).

Research in Arizona (Welch, 1960), Minnesota (Nelson and Mech, 1981), and Georgia (Kammermeyer and Marchinton, 1977) suggests that male white-tailed deer expand their home range during autumn, a behavior attributed to breeding activities (Beier and McCullough, 1990). We found home ranges in summer, prerut, rut, and postrut seasons to be similar, with home ranges in spring being notably small. The lack of expansion of home range during the 6-week rutting season was unexpected, yet supported by concurrent activity measurements (Hellickson, 2002). Beier and McCullough (1990) saw a reduction in size of home range for males during summer and suggested that this may be attributable to social behavior related to fawning or to seasonal increases in availability of forage, such that availability exceeds the increase in metabolic demand (Harestad and Bunnell, 1979). The latter is a more plausible explanation for our observed size of home range in spring because peak fawning occurs in summer rather than spring (Illige, 1951) and availability of forage is greatest following precipitation in spring (Hall, 1997). Similarly, core areas in spring were reduced, suggesting that deer could meet their physiological and nutritional demands within a smaller area during this season.

Fidelity to home range between years was high (≥61% overlap) within all age categories. Deer demonstrated a pattern of increased fidelity to home range with maturation, with fidelity to home range of old deer being greater than

middle-aged deer. Interestingly, fidelity to core area between years exhibited an opposite trend, although age categories did not differ. We suggest that as males mature past prime breeding age, they are less likely to explore and use new areas, becoming more fixed in their use of space among years. Furthermore, we surmise that older-aged deer display increased flexibility in their core areas of activity; perhaps, because they are relegated to alternate areas within their home range by younger, more active deer (Hellickson, 2002). The notably low overlap in core area between years for old deer during the prerut season provides additional support for this.

Elevated fidelity to summer ranges compared to other seasons has been observed by researchers in New York (Tierson et al., 1985), Michigan (Beier and McCullough, 1990; Van Deelen et al., 1998), and Quebec (Lesage et al., 2000). Within these northern populations, variation in migratory (Lesage et al., 2000) or quasi-migratory (Beier and McCullough, 1990) movements to winter ranges is a common explanation. Obviously, this justification does not fit non-migratory populations. Our elevated fidelity between years to home range in summer may be a strategy to avoid nutritional and thermoregulatory stress associated with dry summers. By using traditional areas with a high diversity of woody browse species (Varner et al., 1977; Pollock et al., 1994), males may be better suited to cope with uncertain resources. Alternatively, greater fidelity to home range during summer could be a function of reduced aggression (Thomas et al., 1965) and increased aggregation (Hirth, 1977), thereby facilitating more traditional use of space.

During the rut, males did not expand their home ranges or core areas in search of receptive females, did not decrease fidelity of home range between years, and reduced their rates of activity (Hellickson, 2002), suggesting that males re-

TABLE 3.—Mean (SE) size of range by season (ha; 95 and 50% kernel) of male white-tailed deer (*Odocoileus virginianus*), 11 January 1993–31 May 1995, on the Faith Ranch in southern Texas.

Age	Season														
	Spring (1 April–31 May)			Summer (1 June–30 September)			Prerut (1 October–31 November)			Rut (1 December–10 January)			Postrut (11 January–31 March)		
	95%	Mean (SE)	50% (ha)	95%	Mean (SE)	50% (ha)	95%	Mean (SE)	50% (ha)	95%	Mean (SE)	50% (ha)	95%	Mean (SE)	50% (ha)
	<i>n</i>			<i>n</i>			<i>n</i>			<i>n</i>			<i>n</i>		
Young (1–2 years old)	26	368 (64)	58 (12)	5	590 (273)	103 (54)	5	577 (326)	91 (66)	13	672 (135)	167 (45)	30	579 (68)	100 (13)
Middle (3–4 years old)	34	255 (22)	36 (4)	19	416 (78)	72 (15)	14	439 (167)	80 (29)	19	465 (93)	89 (20)	37	520 (53)	91 (13)
Mature (5–6 years old)	47	252 (21)	42 (5)	29	493 (75)	69 (10)	28	739 (341)	111 (46)	38	492 (52)	93 (9)	49	565 (88)	94 (15)
Old (≥7 years old)	25	249 (31)	36 (5)	23	369 (41)	59 (11)	20	347 (119)	58 (23)	21	372 (57)	69 (10)	27	397 (44)	66 (10)

TABLE 4.—Mean (SE) between-year seasonal home range (95% kernel) and core area (50% kernel) overlap (%; a measure of site fidelity) of male white-tailed deer (*Odocoileus virginianus*), 11 January 1993–31 May 1995, on the Faith Ranch in southern Texas.

Age (during second season of radiomonitoring)	Season														
	Spring (1 April–31 May)			Summer (1 June–30 September)			Pruet (1 October–31 November)			Rut (1 December–10 January)			Postrut (11 January–31 March)		
	95% (SE)	50% (SE)	Mean (SE)	95% (SE)	50% (SE)	Mean (SE)	95% (SE)	50% (SE)	Mean (SE)	95% (SE)	50% (SE)	Mean (SE)	95% (SE)	50% (SE)	Mean (SE)
	<i>n</i>			<i>n</i>			<i>n</i>			<i>n</i>			<i>n</i>		
Young (2 years old)	2	38 (11)	29 (1)										2	43 (2)	4 (1)
Middle (3–4 years old)	10	48 (5)	24 (7)	6	52 (7)	27 (8)	5	45 (7)	16 (10)	4	35 (6)	9 (5)	11	46 (4)	27 (7)
Mature (5–6 years old)	12	51 (5)	26 (6)	7	58 (3)	38 (9)	6	45 (7)	30 (10)	10	41 (3)	21 (4)	11	51 (5)	31 (8)
Old (≥7 years old)	12	45 (6)	24 (6)	9	57 (4)	29 (6)	8	37 (5)	6 (4)	8	38 (6)	20 (7)	12	52 (4)	32 (5)

mained relatively sedentary during this season. However, males reduced fidelity to core areas of activity during the rut between years. We suggest that shifts in core areas during the rut may be in response to variation in availability of receptive females occurring within home ranges of males between years, yet outside their core areas of activity the previous year.

In contrast to a prediction of the subdominant-dominant-floater model, annual home range sizes did not vary among age categories. However, annual home range means followed the predicted pattern, and young and mature deer maintained larger seasonal home ranges than old deer. We conclude that there is some evidence in support of this prediction. Regarding size of home range, young and mature males behaved similar to subdominant and dominant floaters, respectively (Brown, 1971; Inglis et al., 1986).

The second prediction of the subdominant-dominant-floater model is that annual and seasonal fidelity to home range would be less for young and mature deer than middle-aged deer. In general, fidelity to home range by young males during the 2 seasons of monitoring (both $n = 2$) tended to be less (spring $\leq 7\%$ and postrut $\leq 3\%$) than the other age categories, although not statistically different. These limited data seemingly support the subdominant-floater characterization of young deer. Based on data on fidelity to home range, we found no evidence of dominant floaters within mature deer. However, Brown (1971) and Inglis et al. (1986) noted that dominant floaters comprised only a fraction of the mature segment of the population, with most mature males being core animals (i.e., mature deer that form stable fraternity groups). Consequently, our inclusion of all mature males in our analysis of fidelity may have masked the presence of some dominant floaters.

Overall, we found limited evidence supporting the subdominant-dominant-floater model. The occurrence of subdominant and dominant floaters within a population is symptomatic of an intricate social structuring of male deer (Brown, 1971). To manage deer populations with a well-developed age structure for males more effectively, future investigations should focus on relationships between social dominance (e.g., floater versus core deer), body size (or physical condition), and productive processes, such as breeding success.

Landowners and hunters considering, or engaged in, management aimed at promoting a well-developed age structure within male deer, frequently ask biologists about the movements of males, specifically whether mature deer will remain on their property for the opportunity to harvest. The high fidelity to home range between years that we observed for all age categories of males suggests little between-year shifting, with most deer being anchored to a substantial portion of their range. However, our annual home-range sizes, as well as home-range sizes of males from across their geographic range (Miller et al., 2003), exceed the acreage of most private landholdings in Texas. For example, Wilkins et al. (2003) found that 78% of farms and ranches in Texas were < 202 ha. Additionally, yearling males readily disperse from natal ranges, often shifting home ranges long distances in southern Texas (McCoy et al., 2005; Webb et al., 2007). These factors should be considered when formulating management plans and reinforce the benefit of establishing management cooperatives with adjacent landowners (Hamilton et al., 1995).

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